

Mixed-severity fire history at a forest–grassland ecotone in west central British Columbia, Canada

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Abstract. This study examines spatially variable stand structure and fire–climate relationships at a low elevation forest–grassland ecotone in west central British Columbia, Canada. Fire history reconstructions were based on samples from 92 fire-scarred trees and stand demography from 27 plots collected over an area of about 7 km². We documented historical chronologies of widespread fires and localized grassland fires between AD 1600 and 1900. Relationships between fire events, reconstructed values of the Palmer Drought Severity Index, and annual precipitation were examined using superposed epoch and bivariate event analyses. Widespread fires occurred during warm, dry years and were preceded by multiple anomalously dry, warm years. Localized fires that affected only grassland-proximal forests were more frequent than widespread fires. These localized fires showed a lagged, positive relationship with wetter conditions. The landscape pattern of forest structure provided further evidence of complex fire activity with multiple plots shown to have experienced low-, mixed-, and/or high-severity fires over the last four centuries. We concluded that this forest–grassland ecotone was characterized by fires of mixed severity, dominated by frequent, low-severity fires punctuated by widespread fires of moderate to high severity. This landscape-level variability in fire–climate relationships and patterns in forest structure has important implications for fire and grassland management in west central British Columbia and similar environments elsewhere. Forest restoration techniques such as prescribed fire and thinning are oftentimes applied at the forest–grassland ecotone on the basis that historically high frequency, low-severity fires defined the character of past fire activity. This study provides forest managers and policy makers with important information on mixed-severity fire activity at a low elevation forest–grassland ecotone, a crucial prerequisite for the effective management of these complex ecosystems.

Key words: British Columbia; climate–fire interactions; dendrochronology; Douglas-fir; fire ecology; fire severity.

INTRODUCTION

Extensive natural grasslands characterize the arid valley-bottoms of the Fraser, Nicola, and Thompson rivers of interior southern British Columbia (BC). At elevations over 700 m above sea level (asl) in these valleys, however, there is often sufficient moisture to support trees allowing for a gradual transition to forests (Tisdale 1947, Tisdale and McLean 1957, Nicholson et al. 1991). Like forest–grassland ecotones elsewhere, this transition is recognized as a dynamic natural boundary controlled by a complex suite of abiotic and biotic factors including fire, climate, and grazing (Risser 1995, Staver et al. 2011, Hansen and di Castri 2012). An important ecological legacy in the forest–grassland ecotones of interior southern B.C. is the spatial and temporal pattern of historical fires, as the severity of past fires is retained in the demographic patterns of forest structure.

High-frequency, low-severity fires are presumed by many to be responsible for the historical character and extent of the forest–grassland ecotones of interior BC (Lepofsky et al. 2003, Bai et al. 2004). However, mixed-severity fire regimes are increasingly recognized as integral to the long-term ecology of similar dry forests and forest–grassland ecotones in western North America (Arsenault and Klenner 2005, Hessburg et al. 2007, Sherriff and Veblen 2007, Klenner et al. 2008, Perry et al. 2011, Odion et al. 2014, Sherriff et al. 2014). “Mixed-severity” is used to describe both the variability in fire severity over multiple fires at one site, and the variation in burn severity in one fire (Perry et al. 2011). These mixed-severity regimes are generally the product of interactions between top-down climate forcing and bottom-up controls of fuel and topography (Perry et al. 2011, Marcoux et al. 2015, Chavardès and Daniels 2016). Moderate to severe fires kill overstory trees and characteristically allow for the establishment of patchy even-age cohorts under conditions of sufficient seed source and post-fire climate suitable for tree establishment (Oliver and Larson 1990). The resulting heterogeneous forest structure supports diverse habitat, high

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species diversity, and resilience to disturbance (Reich et al. 2001, Peterson and Reich 2008, Heyerdahl et al. 2012). While the same fires are presumed to play a key ecological role in maintaining the adjacent grasslands (Tisdale and McLean 1957, Turner and Krannitz 2001, Sherriff and Veblen 2007), the historical encroachment of trees into these grasslands and conifer infilling of meadows in the forest–grassland ecotone is of growing ecological and economic concern (Covington and Moore 1994, Bai et al. 2004, Klenner et al. 2008).

Within interior BC native grasslands and the forests adjacent to these grasslands, are economically important forage areas for livestock grazing (Bai et al. 2004). In the absence of 20th-century fires, trees such as Douglas-fir (*Pseudotsuga mezesii* var. *glauca* Beissn. Franco), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws), and western juniper (*Juniperus occidentalis* Hook.) are advancing beyond the forest–grassland ecotone to encroach into the adjacent upper elevation grasslands (Strang and Parminter 1980, Turner and Krannitz 2001, Lepofsky et al. 2003, Bai et al. 2004). This encroachment has significantly reduced the available forage area (Turner and Krannitz 2001, Bai et al. 2004) and has many advocating for the application of enhanced management practices to restore their historical character (Klenner et al. 2008, Hessburg et al. 2016). With recent research indicating that prescribed fire and mechanical treatments applied heterogeneously across similar landscapes assists in the restoration of multi-scale structural complexity (Ryan et al. 2013, Hessburg et al. 2016), there is an acute need to establish reference conditions of the prevailing fire regime prior to the initiation of modern land-use practices in the mid- to late 1800s (Landres et al. 1999, Swetnam et al. 1999, Keane et al. 2009).

The goal of this study was to describe landscape-level variability in fire occurrence, stand structure, and fire–climate relationships at a forest–grassland ecotone in west central BC. The intent of the research was to: (1) use dendroecological methods to describe tree establishment histories in forested areas of the study area; (2) characterize wildfire activity in terms of frequency and severity; and (3) document fire–climate relationships. In our paper, we use ecological data derived from dendrochronology and stand demography methods to reconstruct past fire regimes (Falk et al. 2011). Fire-scarred trees preserve an annual and sometimes seasonal record of fire events (Arno and Sneek 1977) and documentation of stand age structure provides insights on the severity of past fires (e.g., Marcoux et al. 2015, Chavardès and Daniels 2016). While we acknowledge that the term “fire severity” can encompass both above-ground and below-ground ecological changes that arise from fire activity (Keeley 2009), in our study we use the term fire severity to describe only the effects of fire activity on forest structure.

Comparable baseline ecological data for historical fire regimes in central interior BC is limited (Daniels and Watson 2003, Heyerdahl et al. 2007, 2008, 2012). Given

this, we hypothesized that frequent, low-severity fires would affect grassland proximal forests (fuel-limited ecosystems) and have a positive relationship with antecedent moisture conditions. We also postulated that historically widespread fires occurred with greater severity across the entire study area and were climatically related to persistent drought-like conditions.

This research provides valuable insight into the response of interior forest–grassland ecosystems to changing climates. Furthermore, the research findings provide information essential for developing future forest management strategies and for designing restoration treatments appropriate to changing climate–fire regimes.

METHODS

Study area

The study area is located in the Churn Creek Protected Area (CCPA) on the Fraser Plateau in west central BC, Canada (Fig. 1). The CCPA was established in 1995 primarily for the conservation of native low-, middle-, and high-elevation bunchgrass grasslands (BC Parks 2000). The adjacent Empire Valley Ranch area was added to the CCPA in 1998. The CCPA now covers almost 37,000 ha of grasslands and interior Douglas-fir forests. It is the largest protected area of native grasslands in BC (Reid 2008, 2010).

The study area encompasses approximately 7 km² within the central CCPA and ranges in elevation from 850 to 1,300 m asl (Fig. 2). The CCPA is located within the rain shadow of the Coast Mountain Pacific Ranges. It typically experiences warm, dry summers and cold, dry winters (Moore et al. 2010). Climate normals (1971–2000) at Big Creek (60 km northwest of the study area) average 13°C in July and –10°C in January. Precipitation totals range from 51 mm of rain in summer months to 25 cm of snowfall in winter months, with 337 mm of precipitation falling annually (Environment Canada 2016).

From 850 to 1,100 m asl the landscape is characterized by relatively flat terrain or gentle east to southeast-facing slopes. The vegetation is a mosaic of grasslands and Douglas-fir forests that shifts in composition in response to local site-specific changes in climate, site, or historical impacts (BC Parks 2000). Grassland vegetation is dominated by bluebunch wheatgrass (*Elymus spicatus*), short-awned porcupine grass (*Hesperostipa spartea*), and spreading needlegrass (*Acnatherum richardsonii*). Forested areas are dominated by Douglas-fir trees, with small pockets of trembling aspen (*Populus tremuloides* Michx.) found in moist depressions. From 1,100 to 1,300 m asl, the landscape is generally flat with a slight southeast-facing aspect. At 1,000–1,100 m asl the upper grassland transitions to a vegetation cover consisting increasingly of Douglas-fir trees. At elevations close to 1,300 m asl Douglas-fir forests dominate, with aspen at moister sites and infrequent lodgepole pine (*Pinus contorta* Dougl.).

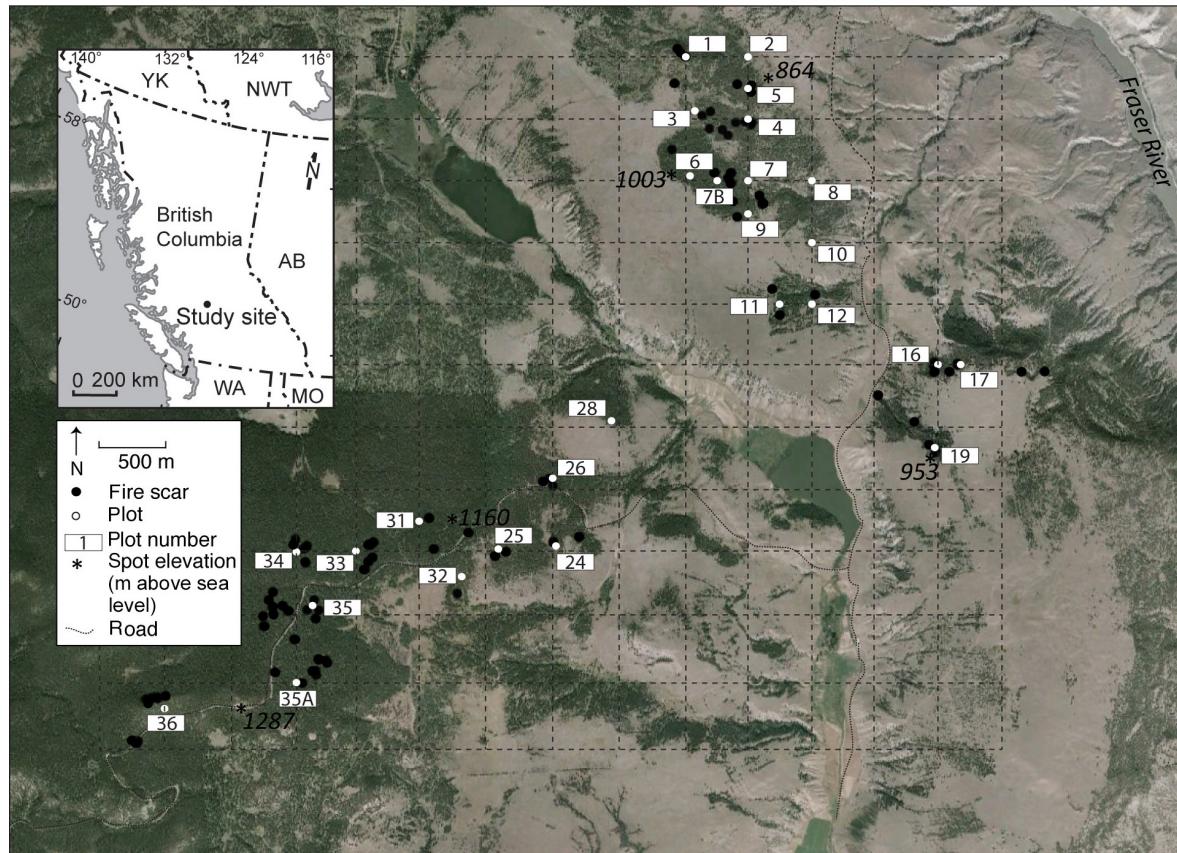


FIG. 1. The Churn Creek Protected Area study site located in west central British Columbia, Canada showing the location of 92 sampled fire-scarred trees and 27 age-structure plots (image from Google Earth). The hatched network is the 500-m grid used to locate the age-structure plots. White circles with numbered boxes represent plot locations and numbers, black circles mark fire-scarred trees sampled in this study, and stars indicate spot elevations in the study area. [Color figure can be viewed at wileyonlinelibrary.com]

At elevations above 1,300 m asl and outside the study area, lodgepole pine intermixes with Douglas-fir and then becomes the dominant montane tree species above 1,500 m asl.

During the twentieth century, Douglas-fir trees encroached into middle and upper grasslands. The character of this encroachment is similar to that elsewhere in BC (Strang and Parminter 1980, Turner and Krannitz 2001, Lepofsky et al. 2003, Bai et al. 2004) and in the western United States (Soulé and Knapp 2000, Heyerdahl et al. 2006). Previous research has documented both pulses and steady infilling of conifer encroachment onto grasslands ascribed to factors that include the reduction in fire occurrence since the early 1900s (Turner and Krannitz 2001, Heyerdahl et al. 2006), and warmer spring temperatures and reduced spring snow depth since the 1970s (Lepofsky et al. 2003). More broadly, 20th-century conifer encroachment into grasslands has been ascribed to combinations of factors including climate, domestic livestock grazing, and the cessation of frequent fire (Bai et al. 2004, Heyerdahl et al. 2006).

Limited archeological evidence shows First Nations activity in the region dates to before 5,000 yr ago (Cybulski et al. 2007, Reid 2008, 2010). Cultural depressions at Big Bar Lake indicate winter occupation of pit-house villages, as well as the procurement of food from local sources (Wilson 1998). Oral histories suggest a traditional use of grassland fires in the region to promote ungulate browsing. Fires were deliberately set in spring to thin understory brush and suppress encroaching sagebrush and conifer seedlings (Turner 1999, Blackstock and McAllister 2004).

Early gold explorers passed through the CCPA in the early to mid-1800s and small placer mines operated in the Empire Valley through the late 1800s (Parminter 1978). Cattle ranching began in the 1860s at Gang Ranch north of the study area, and small herds of cattle have been grazing in the Empire Valley since the end of 19th century. The number of cattle in the Empire Valley varied through the early 1900s, peaking in the 1960s with 2000 head of cattle (BC Parks 2000). Historical logging occurred within parts of the study area in the early 1900s and led to patches of higher-density second-growth stands.



FIG. 2. (A) Landscape view of the study site looking southeast toward Plots 16 and 17. (B) Sample collected from a standing dead Douglas-fir tree at Plot 4. The tree was located about 200 m from expansive grasslands and in a closed-canopy forest. The individual tree records 12 fire events from AD 1620–1896 with an average return interval of 25 yr. [Color figure can be viewed at wileyonlinelibrary.com]

Site selection, field sampling, and sample processing

A 7000-ha area within the CCPA was identified for study (Fig. 1). The area was selected to avoid sites influenced by historical and contemporary logging, as well as areas likely to have been influenced by prescribed fire and thinning activities (BC Parks 2000). As previous research indicates that forest–grassland adjacency is useful to extract climate–fire relationships in grassland environments (Sherriff and Veblen 2008, Gartner et al. 2012), a study area was selected that included mature, grassland-adjacent forests. Field reconnaissance showed that, beyond approximately 400 m from the expansive grasslands characterizing the CCPA, elevation and forest density typically increased.

Plots to determine tree establishment histories in forested areas were located based on a 500-m grid over the study area (see Fig. 1). At sites with minimal forest cover, the density of plots was increased and a 250-m grid was used. Plots were randomly adjusted 50 or 75 m when grid intersection points occurred in areas affected by seasonal roads, absence of forest cover, very steep slopes, and/or evidence of historical logging. An *n*-tree density adapted plot sampling strategy was employed (Lessard et al. 2002, Brown and Wu 2005) where the plot size varies and the nearest 30 standing dead trees, snags, or living trees ≥ 1.7 m in height to the plot center were sampled. Increment borers were used to take two cores ~ 25 cm above the ground surface from trees with a diameter at breast height (dbh) ≥ 7 cm. Basal disks were taken from all trees with a dbh of < 7 cm. At Plot 7, basal

sections were taken from 30 seedlings approximately 25 cm tall to establish a site-level coring–height correction factor (Wong and Lertzman 2001).

To reconstruct fire history records at each plot, one to six fire-scarred trees with the greatest number of scars were identified within circular 1-ha search areas surrounding the center of each plot (Arno and Sneek 1977, Amoroso et al. 2011, Chavardès and Daniels 2016). Scar samples were collected from living trees and standing dead trees, as well as from fallen logs, stumps and coarse woody debris. In addition, fire-scarred trees with well-preserved fire records outside the 1-ha search areas were opportunistically sampled.

Increment cores and fragile cross sections were glued to wooden mounts and allowed to air dry. The samples were sanded with progressively finer grits until the xylem cellular structure was visible under magnification. Both visual and statistical methods (Grissino-Mayer 2001) were used to crossdate all samples against a previously developed master chronology (AD 1490–2009) from nearby Farwell Canyon (Axelson et al. 2015).

Fire scars were dated based on their year of record in crossdated annual rings (Dieterich and Swetnam 1984). Whenever possible, the fire season was assigned on the intra- or inter-ring position of the scar. Each fire was classified as having occurred: during the dormant season; during the time of early-, middle-, or late-earlywood cell development; or, during the formation of latewood cells (Baisan and Swetnam 1990). We interpreted dormant season scars to represent fires that occurred in the late summer or fall following the cessation of seasonal

latewood growth (Caprio and Swetnam 1995). The modern season of peak fire activity supports this convention.

The establishment date of individual trees (living and dead) within each plot was determined from the increment cores or basal disks by annual ring counts and crossdating (Grissino-Mayer 2001). Correction factors were employed to account for cores that missed the pith and to adjust for sampling height error (Sigafoos and Hendricks 1969). In the case of off-center cores, a geometric model was used to estimate the number of rings to the pith (Duncan 1989). To correct for coring height, the average age of 30 seedlings 25 cm tall was added. No correction factors were applied to the basal disks.

Fire history, frequency, and severity

Two fire chronologies were reconstructed. One chronology was constructed from fires that scarred at least 25% of recording samples across the entire study area and at least two trees recording the fire event (referred to hereafter as “widespread fires”). Fire dates from samples located within 400 m of grasslands and that scarred at least 10% of recording trees (and at least two trees recording the fire event) were composited into a second chronology (referred to hereafter as “grassland fires”). The grassland fire chronology included all fire years that affected the forest–grassland ecotone. To exclude modern human influences on local fire regimes, fire events after AD 1900 were removed from the fire chronologies.

Fire severity was inferred from stand demography reconstructed from the establishment plots. The establishment of even-aged Douglas-fir forest cohorts within interior BC characteristically follows disturbance resulting from fires, insect outbreaks, and windthrow events (Heyerdahl et al. 2012). For this study, a cohort was identified if five or more trees (also $\geq 25\%$ of trees) established within a 20-yr period, preceded by a 30-yr period over which no trees established (Heyerdahl et al. 2012, Chavardès and Daniels 2016). Fire events recorded on samples within 150 m of a plot were then compared to the intervals of establishment (cohorts) for that plot (Brown et al. 2008, Heyerdahl et al. 2012). We found that including samples taken from fire-scarred trees within 150 m of each plot improved the length and replication of fire events for the plot-level fire history reconstructions. Due to the presence of abundant fire scars, soil charcoal and charred coarse woody debris within the even-aged cohorts examined in the CCPA, it was postulated that all developed following fire events. While we recognize that cohorts can establish following other disturbances including insect outbreaks and windthrow (Axelson et al. 2009), we did not find any evidence of historical stand-altering insect or windthrow events. Following Heyerdahl et al. (2012) we visually compared cohort establishment dates with those captured by the Palmer Drought Severity Index (PDSI) reconstruction to determine whether seedling establishment events followed intervals of cool and (or) wet climate conditions.

The presence of fire scars and even-aged cohorts were used to assign each plot to one of three classes of fire severity (Heyerdahl et al. 2012, Chavardès and Daniels 2016). Low-severity fire plots were assigned using the following criteria: (1) where there was scar evidence of multiple fire years and the presence of a cohort originating after only the last fire or (2) when a plot contained trees with variable establishment dates and no visible fire scars. Criteria for historic mixed-severity fire plots included: (1) the presence of multiple fire scar years and two or more even aged-cohorts or (2) the presence of multiple fire scar years and a cohort that was affected by subsequent fires. High-severity fire activity was identified at plots with no fire-scarred trees and an even-aged cohort.

Climate data

We relied on tree-ring derived proxy indices of the PDSI and precipitation to analyze fire–climate relationships from AD 1600–1900 (Cook et al. 2004, 2008, Watson and Luckman 2004). Negative PDSI values in June–August describe warm and dry conditions, whereas positive values indicate wet, cool conditions (Cook et al. 2004). In our analysis, we used reconstructed PDSI values from Gridpoint 30 (120 km north of the study area, 805 m asl; Cook et al. 2008). We removed autocorrelation from the PDSI time series by fitting an autoregressive integrated moving average model of an order determined based on Akaike’s Information Criterion (Heyerdahl et al. 2008, Flower et al. 2014). A reconstruction of annual precipitation (previous June to current July) at Big Creek, BC, was also employed (Watson and Luckman 2004). Big Creek is located 55 km northwest from the study area and at a similar elevation (1,130 m asl). Autocorrelation was not detected in the precipitation time series.

Fire–climate relationships

Superposed epoch analysis (SEA) and bivariate event analysis (BEA) were used to evaluate for associations between the fire chronologies and climate variability. Climate–fire studies commonly use SEA to elucidate inter-annual relationships between fire occurrence and climate over short intervals (3–5 yr; Grissino-Mayer and Swetnam 2000, Trouet et al. 2010). BEA has also been employed in fire–climate research (e.g., Gartner et al. 2012, Rother et al. 2014) to assess interactions between fire activity and extreme climate events over variable windows of analysis (e.g., 10–30 yr; Gavin et al. 2006, Gavin 2010).

We used SEA to determine if the mean value of the climate reconstruction differed significantly in each year before ($t = -1$ to -4), during ($t = 0$), and after fire events ($t = +1$ to $+4$). Confidence intervals of 95% and 99% were developed using bootstrapping methods to assess statistical significance. The pre-whitened anomalies of PDSI

and the precipitation reconstruction were used in the SEA. BEA was conducted in K1D software (Gavin 2010), and extreme climate years were defined as those where the index value was at least one standard deviation (positive or negative) from the mean (Rother and Grissino-Mayer 2014). We transformed bivariate Ripley's K -function to the L function to stabilize the mean and variance and improve result interpretation (Gavin et al. 2006, Gavin 2010). Forward selection was used in the K1D software, where fire events were preceded by extreme climate years, and we generated 95% confidence intervals based on 1,000 randomized Monte Carlo simulations. Values of the L function that exceed the upper confidence interval indicate a strong relationship of fire events t years after the extreme climate years. Values of the L function that fall below the lower confidence interval indicate fire–climate asynchrony at t years after the extreme climate years. L function values between the confidence intervals indicate fires occur independently of extreme climate years.

RESULTS

Fire history, frequency and severity

Partial cross sections from 98 fire-scarred Douglas-fir trees allowed for identification of 437 individual fire scars. Six samples were excluded from analysis due to substantial decay. The majority of fire scars (73%) were identified at the boundary between latewood and earlywood. The ring position of the remaining scars was undetermined (16%), within the latewood (7%), or in the late portion of the earlywood (3%). Very few scars were identified in the early or middle portion of the earlywood ($n = 5$, <1%).

A total of 14 unique widespread fire events and 28 unique grassland fire events were identified from AD 1600 to 1900 (Fig. 3). Composited fire return intervals were calculated to broadly characterize fire frequency at

the plot level (including 150 m search areas; Table 1). After ~AD 1896, wildfire activity decreased, coinciding with the advent of cattle grazing, fire suppression, and mineral exploration in the region.

Twenty-seven stand demography plots were established. Twenty plots were located at or near the intersection points of the 500-m grid and seven plots were located at or near the intersection points of the 250-m grid (Fig. 1). The locations of 10 plots were adjusted from grid intersection points due to seasonal roads, absence of forest cover, very steep slopes, and/or evidence of historical logging.

We sampled 810 trees in the 27 plots. The plot radius varied from 10 to 17 m and the average plot size was 0.03 ha. Pith was missed on 76% of cores, with between 1 and 15 rings added using the method described (Duncan 1989). Samples were excluded if more than 15 rings were needed to correct for pith ($n = 31$) or if establishment dates of dead trees could not be found using cross-dating methods ($n = 56$). To correct for coring height, the average age (23 yr; range 15 to 33 yr; standard deviation 4.6) of 30 seedlings was added to the earliest year of each tree core.

Trees in five plots had multiple fire scar years and a cohort established in the mid- to late 1800s following the last recorded fire located within 150 m of the plot (Fig. 4). One plot (Plot 6) had no fire scars or even aged-cohorts, but did exhibit variable tree establishment over 400 yr (Fig. 4). Three plots had multiple cohorts and multiple fire scars (Plots 1, 3, and 9). The majority of plots ($n = 13$) had a single cohort established in the mid-1800s and a record of multiple fires before and after the cohort established. Three plots had no fire scars and the presence of one even-aged cohort (Plots 2, 10, and 28) or no cohort (Plot 8; Fig. 4). One plot (Plot 11) had one fire event recorded on one tree and one cohort. None of the cohorts examined showed a relationship between establishment and intervals of cool and wet climate conditions.

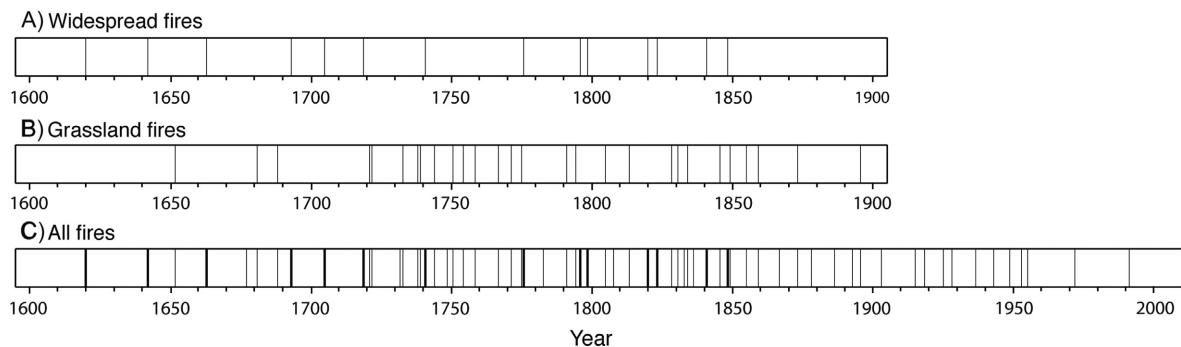


FIG. 3. (A) Widespread and (B) grassland fire chronologies between AD 1600 and 1900 used in these analyses. Widespread fire years were identified when fire was recorded by at least 25% of recording samples over the entire research area. Grassland fires were identified as fires that scarred at least 10% of recording samples (and ≥ 2 samples) within 400 m of grasslands. (C) All fires recorded in the study area between AD 1600 and 2010. Fires that occurred between AD 1901 and 2010 were not included in the analyses. Widespread fires are shown with thicker lines.

TABLE 1. Fire record characteristics for the 27 plots in the study area.

Plot	Fire record years	No. fire scars	No. cohorts	No. fire return intervals	Mean return interval (yr)	Range of return interval (yr)	Fire regime severity	First fire year†	Last fire year†
1	1677–2012	2	2	8	23	7–62	mixed	1741	1925
2	–	0	1	–	–	–	not determined	–	–
3	1587–2012	3	2	11	20	4–39	mixed	1620	1841
4	1588–2012	4	1	19	16	1–33	mixed	1620	1927
5	1601–1989	2	1	10	18	4–40	low	1681	1863
6	–	0	1	–	–	–	low	–	–
7	1592–2012	2	1	7	33	11–70	low	1663	1896
7B	1600–1983	2	1	15	16	3–29	mixed	1620	1859
8	–	0	0	–	–	–	not determined	–	–
9	1712–2012	4	2	16	13	2–41	mixed	1722	1937
10	–	0	1	–	–	–	high	–	–
11	1719–2012	1	1	‡	‡	‡	not determined	1859	1859
12	1755–1950	1	1	2	47	46–47	low	1813	1896
16	1689–2012	4	1	14	11	1–34	mixed	1699	1859
17	1680–2012	3	1	7	20	1–47	mixed	1754	1896
19	1550–1964	1	1	2	69	61–76	low	1722	1859
24	1689–2012	1	1	5	48	26–74	mixed	1693	1925
25	1609–2012	3	1	8	37	12–104	mixed	1663	1955
26	1784–2012	3	1	7	6	1–11	mixed	1820	1863
28	–	–	1	–	–	–	high	–	–
31	1741–2012	2	1	10	11	5–22	mixed	1776	1886
32	1780–1926	1	1	4	18	10–29	low	1792	1865
33	1640–2012	4	1	14	16	6–42	mixed	1642	1897
34	1606–2012	6	1	17	15	3–88	mixed	1693	1955
35	1520–2012	4	1	17	22	8–58	mixed	1586	1955
35A	1689–2001	5	1	11	16	2–81	mixed	1783	1958
36	1665–2012	4	1	8	18	2–36	mixed	1705	1848

Notes: – indicate that there is no fire history data available for that plot.

† Years when fire was recorded by ≥ 1 tree in plot.

‡ Only one fire year documented in this plot.

Fire–climate relationships

Statistically significant relationships were identified between fire years, PDSI, and precipitation using SEA (Figs. 5 and 6). Years of widespread fires ($t = 0$) were significantly associated with dry and warm years ($P < 0.01$; Fig. 6). Grassland fires were not significantly associated with dry warm years in the fire year ($t = 0$), but were significantly associated with cooler, wetter conditions ($P < 0.05$; Fig. 6) in the year preceding the fire ($t - 1$). In years with no fire ($n = 238$), SEA indicates conditions were cooler and wetter ($P < 0.05$).

Statistically significant relationships were found using BEA between extreme PDSI and precipitation years, and widespread and grassland fire events (Fig. 7). Widespread fire years were synchronous with negative extreme PDSI years during the fire year and nine years preceding the fire. Widespread fires were also synchronous with dry conditions (negative extreme precipitation years) in the year of the fire ($t = 0$) and the year preceding the fire ($t - 1$). While widespread fires were not related to positive PDSI and positive precipitation extreme years, grassland fires were synchronous with positive PDSI extreme years in the year of the fire ($t = 0$) and positive precipitation extreme years in the year of the fire and

year preceding the fire ($t = 0$, $t - 1$). To summarize, BEA revealed that widespread fires were in-phase with negative, extreme PDSI and precipitation years but out of phase with positive, extreme PDSI and precipitation years. Grassland fires were in-phase with positive, extreme PDSI and precipitation years and out of phase with negative, extreme PDSI and precipitation years.

DISCUSSION

Fire history

Between AD 1600 and 1900 the study area was affected by 14 widespread fires. Twenty-eight smaller fires were recorded on at least two scarred trees located at or near grassland areas over the same interval (Figs. 4 and 5). Similar to research in the adjoining Cariboo-Chilcotin region that reported a mean fire interval of 27 yr (AD ~1600–1988; ~1 ha search areas; Daniels and Watson 2003), our data describes a mean fire interval of 23 yr averaged across the 21 plots with two or more fire scars (Table 1). The limited number of grassland fires recorded from AD 1600 to 1700 is attributed to the low number of >300 yr old fire-scarred trees found within the local forest–grassland ecotone.

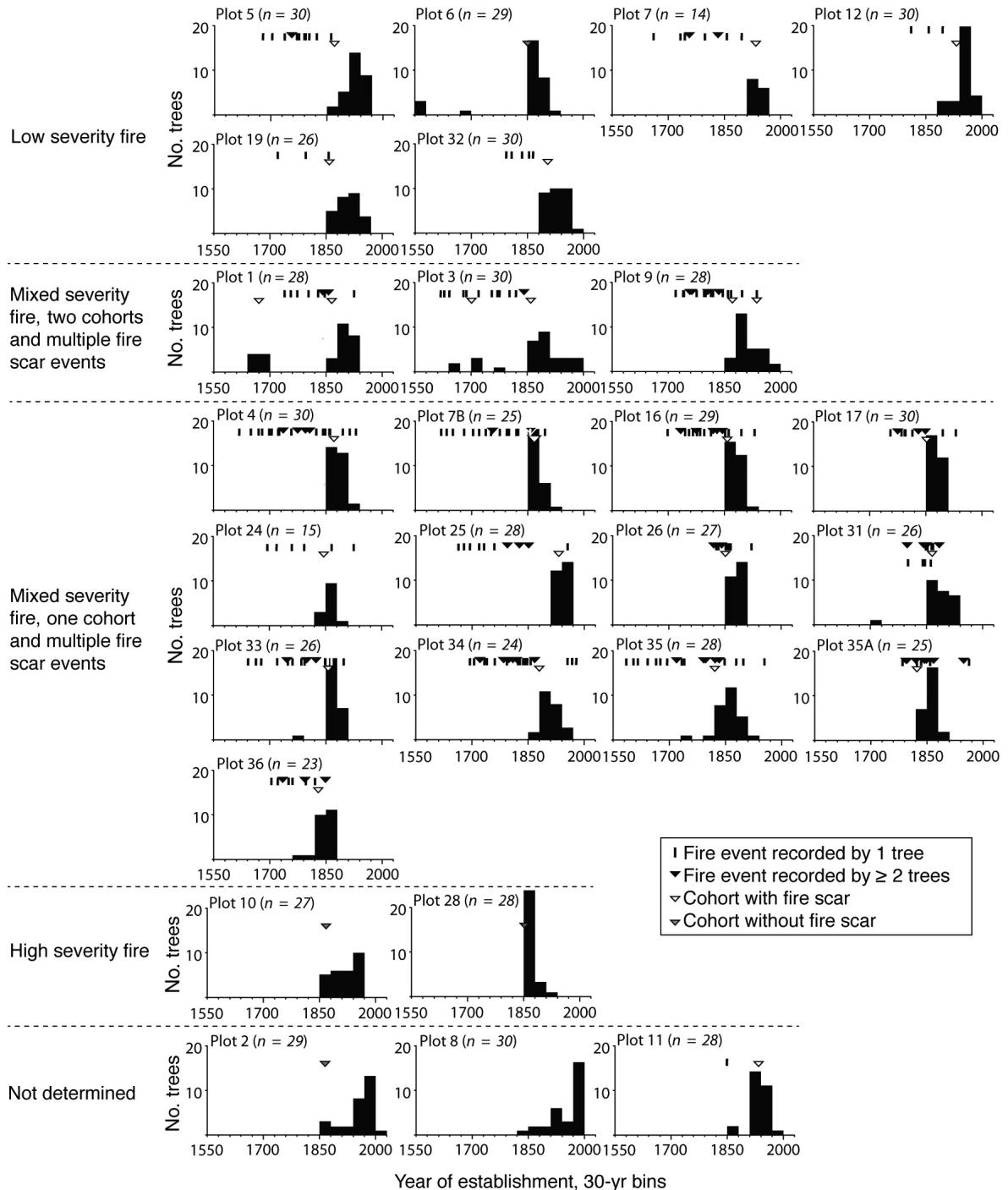


FIG. 4. Fire history reconstructed from fire scars and post-fire even-aged cohorts for the 27 plots. The x-axis of each histogram records the year of tree establishment in 30-yr bins and the y-axis measures the number of live and dead trees crossdated from each plot (total number of trees in each plot given in parentheses). Cohorts are marked by the establishment date of the youngest tree in the cohort.

The majority of fire scars were identified at the boundary between latewood and earlywood cells. This observation suggests most fires occurred in late July to early August at or near the cessation of the latewood growth

season. In contrast, spring fires recorded in the earlywood were very few (4% of scars). One notable exception is the widespread fire of AD 1820 that scarred 32% of the middle- to late-earlywood or latewood cells of

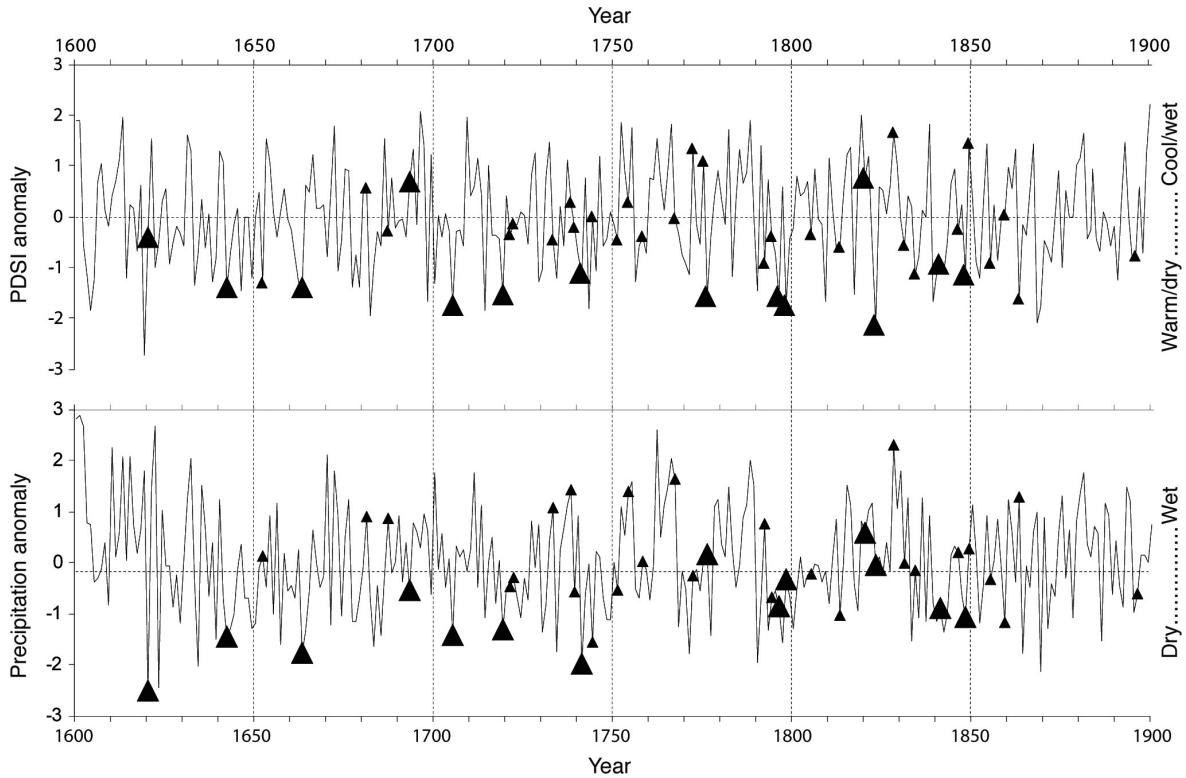


FIG. 5. Fire and climate relationships from AD 1600–1900. Widespread fire years (large triangles) were identified where fire was recorded by at least 25% of samples over the entire research area. Small triangles mark localized fires within 400 m of grasslands (where at least 10% of recording samples (and ≥ 2 samples) were scarred). Lines designate annual tree-ring reconstructed PDSI (Palmer Drought Severity Index; Cook et al. 2008) and precipitation (Big Creek; Watson and Luckman 2004) anomalies. General gradients of climate conditions associated with each climate reconstruction are on the right-hand axis (Watson and Luckman 2004, Cook et al. 2008).

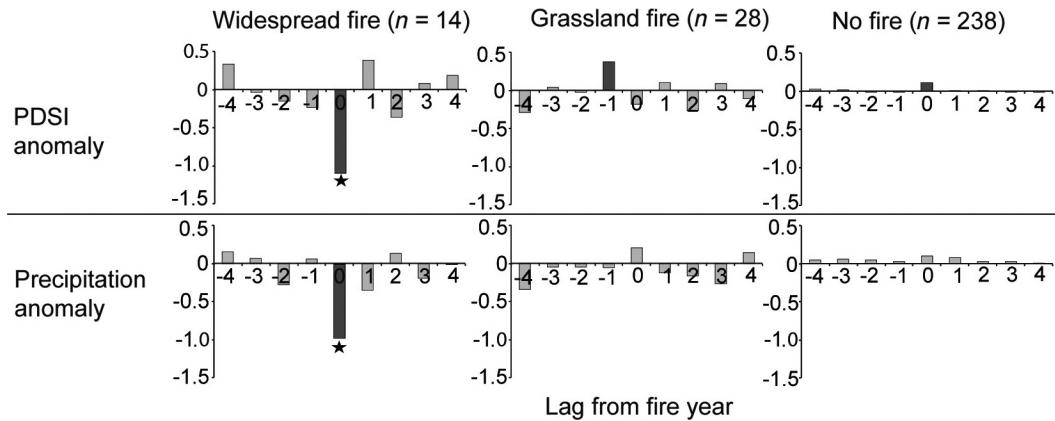


FIG. 6. Lagged interannual relationships of climate and fire from AD 1600–1900, showing mean departures (standard deviations) from climate during 14 yr with widespread fire, 28 yr with localized grassland fire, and 238 yr with no fires for years before ($t = -1$ to -4), during ($t = 0$) and after ($t = +1$ to $+4$) fire or no fire years. Climate records included in analysis include the Palmer Drought Severity Index (gridpoint 30; Cook et al. 2008), and precipitation (Big Creek; Watson and Luckman 2004). Temporal autocorrelation was removed from the PDSI time series using an ARMA model of an order determined based on Akaike's Information Criterion. Dark grey shading shows the fire relationships with statistically significant (at the 95% confidence interval) anomalies. Stars indicate statistical significance at the 99% confidence interval.

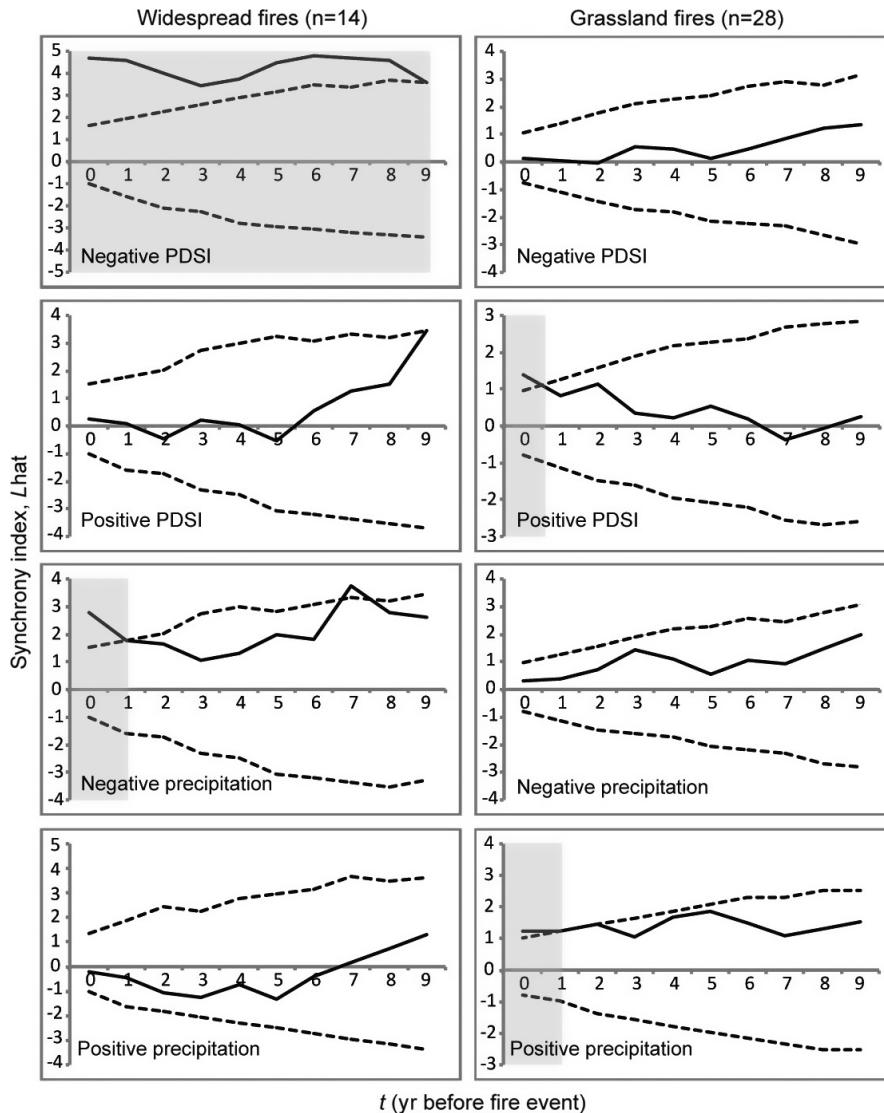


FIG. 7. Bivariate event analysis of the temporal association of extreme negative and positive Palmer Drought Severity (PDSI; Cook et al. 2008) and precipitation (Watson and Luckman 2004) years with fire in CCPA (AD 1600–1900). Extreme climate events were defined using a threshold based on ± 1 SD. Black solid lines indicate L_{hat} values (L function with stabilized mean and variance) for t years before the fire events ($t = 0$). Dotted lines indicate the upper and lower confidence intervals (95%). L_{hat} values outside the confidence intervals indicate synchrony with fire, and values between the confidence intervals indicate a random relation of fire and climate events. Grey shaded bars highlight statistical significance ($P < 0.05$).

recording samples. As regional fires were scarce in the spring of AD 1820 (Iverson et al. 2002, Daniels and Watson 2003, Heyerdahl et al. 2007, 2008, 2012), and the reconstructed PDSI and precipitation records do not indicate anomalously dry conditions (Fig. 5), we speculate that First Nations burning or heightened lightning activity may explain this unusual widespread fire event.

Fire severity

The forest structure data indicate that stands throughout the study area experienced both frequent, stand-maintaining fires and widespread, stand-altering fires. At

seven plots, we found evidence of low-severity fires. In five of the low-severity plots, we postulate that a cohort established after the last fire and, in the absence of subsequent fires, grew to dominate the forest structure. These plots were mostly located in low-density forest stands found adjacent to (within 50 m) or surrounded by grasslands (Fig. 1). Plot 6 exhibited multi-aged stand structure. Although no fire-scarred trees were located within 150 m of Plot 6, consideration was given to multiple fire-scarred trees recording many fire events within 300 m of Plot 6.

The criteria used to identify mixed-severity plots describe a history of frequent fire events (range 6–20

events) between AD 1600 and 1900 generally indicative of low-severity fires, but punctuated by fire(s) of greater severity as reflected by the presence of one or two even-aged cohorts ($n = 16$ Plots; Fig. 4). Cohorts that established in the mid- to late 1800s were affected by subsequent low- to moderate-severity fires. Multiple fire events and single cohorts were identified at 13 plots (Fig. 4). Multiple cohorts and fire events were documented at three plots (Plots 1, 3 and 9; Fig. 4) suggesting the occurrence of at least two stand-altering fires of moderate to high severity leading to the establishment of two even-aged cohorts. Instances where fire (recorded by ≥ 2 scarred trees) and a cohort were identified in the same plot suggests that three fires (AD 1798, 1841, 1848) were severe enough to cause tree mortality and the subsequent initiation of a new cohort of trees (Fig. 4 and Appendix S1; Fig. S1).

The fire history of Plots 10 and 28 reflects high-severity fire activity (Fig. 4). The absence of fire scars and the establishment of a cohort of the oldest trees suggests that a high-severity fire caused substantial overstory mortality. This mortality would have improved the light and nutritional space for survivors, as well as for seedling establishment and growth.

Last, the fire severity of three plots (Plots 2, 8 and 11) located next to grasslands was not determined (Fig. 4). Plots 2 and 8 had variable tree establishment dates and no fire scars. Plot 11 had a single fire event recorded by one tree and an even-aged cohort. At these plots the stands contained many young trees suggestive of grassland infilling in the absence of fire and not high-severity fire effects.

The impact of fire suppression on contemporary stand structure was difficult to quantify as fire has generally been absent on this landscape for the past 100 yr with the exception of small isolated fires (e.g., 1925, 1927, and 1955). In the absence of fire, forest density increased over the past century and the interval between fire events at the end of the 19th century lengthened (Fig. 3). This has been reported for other forest/grassland ecotones in western North America (Veblen et al. 2000). It is worth noting that our classification of fire severity could have been affected by this change in forest structure and fire frequency. The result would be underrepresentation in the number of plots dominated by only low-severity fire and inflation in the number of plots classified as mixed-severity fire history. In order to reduce this source of uncertainty, we recommend in the future increasing the number of overstory trees sampled in each plot and applying a stratification by age class.

Fire-climate relationships

Our results show that fires affecting the CCPA forest-grassland ecotone are controlled by both climate (top-down factors) and fine fuel development (bottom-up factors). Superposed epoch analysis of PDSI and precipitation indicates that widespread fires occurred during

anomalously dry, warm years (Fig. 6). Bivariate event analysis supports this finding and adds that dry, warm conditions over multiple years precede widespread fires (Fig. 7). Extended droughts likely reduced the moisture content of forest fuels across the entire study area. The increased availability of dry fuels would have facilitated the spread of fire across the landscape, leading to widespread fire events (Miller and Urban 2000). During years of less extreme drought, pockets of vegetation with greater moisture content would have persisted, hindering the spread of fire. The association between extended drought conditions and widespread fires in similar settings is well known (e.g., Collins et al. 2006, Heyerdahl et al. 2008, Morgan et al. 2008). For example, in the southern interior of BC and within the inland areas of the northwestern United States, widespread fires from AD 1650 to 1900 characteristically burned in years with above-average warm, dry spring and summer conditions (Heyerdahl et al. 2008). More specifically, Daniels and Watson (2003) found significant relationships between major fire events and below-average precipitation in the year of the fire in southern interior BC.

Grassland fires in the CCPA were found to be associated with wetter, cooler conditions in the year of the fire and the year preceding the fire. This climatic association suggests that cool, wet spring and early summer conditions may promote the growth and productivity of the herbaceous layer, thereby increasing the availability of fine fuels that would assist the spread of fire in grassland environments (i.e., Miller and Urban 2000). During the peak fire season (July and August) conditions are generally hot and dry every year, which would dry the denser fine fuels. However, considering that we did not find a relationship between dry, warm conditions during the fire year and the occurrence of grassland fires, we suggest that pockets of fuel remained sufficiently moist to restrict the spread of grassland fires to smaller patches. The association between fires affecting grassland proximal forests and antecedent moisture conditions has been documented in similar environments (Westerling et al. 2003, Sherriff and Veblen 2008, Gartner et al. 2012).

Mixed-severity fire from stand structure and fire-climate relationships

Grassland proximal forests are generally thought to be affected by low-severity, high-frequency fires (Agee 1996, Swetnam and Baisan 1996; Everett et al. 2000, Hessburg et al. 2005). However, our findings suggest that the contiguous landscape pattern of forest structure in the study area reflects variable fire behavior and frequency between AD 1600 and 1900. At three plots, we document the presence of multiple cohorts and fire scars, indicating that fires burned with differential severity at the plot level. We also found evidence of variability in the burn severity of one fire. For instance, Plot 28 records the establishment of 21 trees over 19 yr beginning in AD 1852. No fire-scarred trees were found within

500 m of Plot 28. By contrast, Plot 26 located ~700 m from Plot 28 contains an even-aged cohort that established from AD 1852 to 1872. Multiple fire-scarred trees within 150 m of Plot 26 record fire events in AD 1820 and 1841. These findings indicate that the behavior of fire in AD 1820 and/or 1841 caused high-severity, stand-replacing fire effects at Plot 28, and moderate-severity fire effects at Plot 26.

The partitioning of widespread fires and grassland fires and the associated respective climate factors illustrates the complex interconnectedness of climate, fuel, fire behavior, and effects. At the site or landscape scale, the documentation of mixed-severity historical fire using the relationships between chronologies of fire events (e.g., widespread and grassland fires) and climate variables has received little attention. The combined insights provided by the landscape pattern of forest structure and fire frequency, and the variable fire–climate relationships, provide convincing evidence of a historic mixed-severity fire history at our study site.

Management implications

Lower density forests dominated the CCPA historically. In the study area between AD 1800–1900, 33 fires were recorded on at least two fire-scarred trees, whereas only 12 fires were recorded between AD 1900 and 2012. Increased human occupation and fire suppression in the 20th century has reduced the number and size of fires affecting the CCPA. As a result, conifer encroachment into the middle and upper grasslands and forest density is increasing since AD 1900 (Fig. 4) and presents ecological implications for the management of the CCPA and similar environments in west central BC. Between AD 1965 and 2001, comparisons of aerial photographs suggests conifers encroached on approximately 200 km² of grassland, or 11% of grassland areas, in the Cariboo Forest Region of BC (Grassland Strategy Working Group 2001). Grasslands, and forests adjacent to grasslands with important grass understory components, in BC and elsewhere are economically important environments for livestock grazing. Conifer encroachment into grasslands reduces grass forage and grazing area for cattle. In addition to livestock grazing, native ungulate species such as white-tailed and mule deer and big horn sheep rely on grasslands and open forests for food and shelter. First Nations in the region use native grasslands for hunting and to harvest traditional foods and medicines (Turner 1999).

The sample in Fig. 2 was collected near Plot 4 and records 12 fire events between AD 1642 and 1896. While the tree from which the sample was collected is located in a closed canopy forest surrounded by younger trees, the high frequency of fires recorded by the tree suggest Plot 4 was historically open and dominated by a few scattered mature trees with little understory. In the event of fire, dense forests can fuel high-severity fires and cause overstory mortality. The loss of mature forests

negatively impacts both the economic and ecological forest values including timber resources, habitat, and species diversity.

A government-led prescribed burning and thinning program has operated in the CCPA since 2000 (Blackwell et al. 2001). The intent is to promote the health of native grasslands by reducing conifer encroachment, enhance the habitat of native grass and animal species, and reduce the spread of noxious weeds (BC Parks 2000). Our research documents frequent historical fire in the CCPA and lends support to these management activities. However, our record of widespread fires between AD 1600 and 1900 suggests that, in order to maintain the natural range of variability of fire activity and stand structure in the study area, forest and grassland management activities should be expanded to include treatments to mimic patches created by high-severity fire to increase stand-level heterogeneity (Churchill et al. 2013).

Hierarchical forest management plans that incorporate prescriptions at the tree, patch, stand, and landscape levels and are based on promoting disturbances and succession to guide ecological change, will be necessary to increase ecosystem connectivity and capacity for resilience under a changing climate (Miller et al. 2007; Hessburg et al. 2015). At the individual tree level, the CCPA contains many large and old Douglas-fir trees that dominate the canopy and have survived multiple fires and droughts while providing reproductive resources for centuries. Restoration activities should prioritize the preservation of these veteran living and dead trees to promote resilience and protect valuable habitat (Hessburg et al. 2015). The application of patch-level prescriptions to mimic tree clump and gap variability would ensure these dry to mesic mixed- and single-species conifer forests are managed to promote heterogeneity.

CONCLUSION

We used two approaches to document historical fire events in the CCPA of both low and moderate to high severity within the forest–grassland ecotone. The use of both fire–climate relationships and stand structure represents a robust approach to identifying and understanding the factors driving fire severity at the landscape scale. Understanding the relationships between climate and fire in the past, and contextualizing these relationships for the future in the face of climate change, necessitates caution. Patterns identified historically may not directly apply to future climate scenarios, but can provide crucial insights. Given the projected increase in temperature in BC and elsewhere over the next 50–100 yr, drought and fire will be prevalent on the landscape. Fire suppression and changes in human land use have led to an increase in tree density, which in turn could lead to more severe fires (Schoennagel et al. 2004).

Managing for heterogeneous forests and landscapes will promote ecosystem and socioenvironmental resilience (Hessburg et al. 2016). Considering forest disturbances

including fire, forest insects, and drought are anticipated to increase in frequency, area, and duration (Turner 2010), adaptive forest management frameworks to buffer both climatic- and human-driven ecosystem change are required (Campbell et al. 2009). Efforts to restore forests and mimic natural disturbance history through prescribed burning and thinning are ongoing in Canada and the United States (Hessburg et al. 2016). Understanding historical fire–climate–fuel relationships can provide valuable insights to the design and application of restoration strategies such as prescribed fire at the forest–grassland ecotone (Schoennagel et al. 2004, Agee and Skinner 2005).

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LITERATURE CITED

- Agee, J. K. 1996. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.
- Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211:83–96.
- Amoroso, M. M., L. D. Daniels, M. Bataineh, and D. W. Anderson. 2011. Evidence of mixed-severity fires in the foothills of the Rocky Mountains of west-central Alberta, Canada. *Forest Ecology and Management* 262:2240–2249.
- Arno, S. F., and K. M. Sneek. 1977. A method for determining fire history in coniferous forests of the mountain west. USDA Forest Service General Technical Report INT-42. Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Arsenault, A., and W. Klenner. 2005. Fire regime in dry-belt forests of British Columbia: perspectives on historic disturbances and implications for management. Pages 105–121 in L. Taylor, J. Zelnik, S. Cadwal-Lander, and B. Hughes, editors. *Mixed Severity Fire Regimes: Ecology and Management Symposium Proceedings*, November, 17–19. Association of Fire Ecology, Spokane, Washington, USA.
- Axelson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management* 257:1874–1882.
- Axelson, J. N., D. J. Smith, L. D. Daniels, and R. I. Alfaro. 2015. Multicentury reconstruction of western spruce budworm outbreaks in central British Columbia, Canada. *Forest Ecology and Management* 335:235–248.
- Bai, Y., K. Broersma, D. Thompson, and T. J. Ross. 2004. Landscape-level dynamics of forest-grassland transitions in British Columbia. *Rangeland Ecology and Management* 57:66–75.
- Baisan, C. H., and T. W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. *Canadian Journal of Forest Research* 20:1559–1569.
- BC Parks. 2000. Management Plan for Churn Creek Protected Area. BC Ministry of Environment, Lands and Parks. http://www.env.gov.bc.ca/bcparks/explore/parkpgs/churn_crk/Management
- Blackstock, M. D., and R. McAllister. 2004. First Nations perspectives on the grasslands of the Interior of British Columbia. *Journal of Ecological Anthropology* 8:24–46.
- Blackwell, B. A., F. Steele, R. W. Gray, K. Iverson, and K. MacKenzie. 2001. Fire management plan Churn Creek Protected Area. BC Parks, Cariboo District, British Columbia, Canada.
- Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86:3030–3038.
- Brown, P. M., C. L. Wienk, and A. J. Symstad. 2008. Fire and forest history at Mount Rushmore. *Ecological Applications* 18:1984–1999.
- Campbell, E. M., S. C. Saunders, K. D. Coates, D. V. Meidinger, A. Mackinnon, G. A. O'Neill, D. J. Mackillop, S. C. Delong, and D. G. Morgan. 2009. Ecological resilience and complexity: a theoretical framework for understanding and managing British Columbia's forest ecosystems in a changing climate. Technical Report 055. BC Ministry of Forests and Range, Victoria, British Columbia, Canada.
- Caprio, A. C., and T. W. Swetnam. 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. United States Department of Agriculture Forest Service General Technical Report INT. Pages 173–179 in J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, technical coordinators. *Proceedings: Symposium on Fire in Wilderness and Park Management*, Missoula, Montana, March 30–April 1, 1993. General Technical Report INT-GTR-320. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Chavardès, R. D., and L. D. Daniels. 2016. Altered mixed-severity fire regime has homogenized montane forests of Jasper National Park. *International Journal of Wildland Fire* 25:433–444.
- Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management* 291:442–457.
- Collins, B. M., P. N. Omi, and P. L. Chapman. 2006. Regional relationships between climate and wildfire-burned area in the Interior West, USA. *Canadian Journal of Forest Research* 36:699–709.
- Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term aridity changes in the Western United States. *Science* 306:1015–1018.
- Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko and D. W. Stahle. 2008. North American summer PDSI reconstructions, Version 2a. http://www.ncdc.noaa.gov/paleo/pdsi08_ts.html
- Covington, W. W., and M. M. Moore. 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry* 2:153–181.
- Cybulski, J. S., A. D. McMillan, R. S. Malhi, B. M. Kemp, H. Harry, and S. Cousins. 2007. The Big Bar Lake Burial: middle period human remains from the Canadian Plateau. *Canadian Journal of Archaeology* 31:55–78.
- Daniels, L. D. and E. Watson. 2003. Climate–fire–vegetation interactions in Cariboo forests: a dendrochronological analysis. Forest Innovation and Investment Research Program, Vancouver, British Columbia.

- Dieterich, J., and T. W. Swetnam. 1984. Dendrochronology of a fire-scarred ponderosa pine. *Forest Ecology and Management* 30:238–247.
- Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrydium dacrydioides*). *New Zealand Natural Sciences* 16:31–37.
- Environment Canada. 2016. 1971–2000 climate normals. http://climate.weather.gc.ca/climate_normals/index_e.html
- Everett, R. L., R. Schellhaas, D. Keenum, D. Spurbeck, and P. Ohlson. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *Forest Ecology and Management* 129:207–225.
- Falk, D. A., E. K. Heyerdahl, P. M. Brown, C. Farris, P. Z. Fulé, D. McKenzie, T. W. Swetnam, A. H. Taylor, and M. L. Van Horne. 2011. Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9:446–454.
- Flower, A., D. G. Gavin, E. K. Heyerdahl, R. A. Parsons, and G. M. Cohn. 2014. Western spruce budworm outbreaks did not increase fire risk over the last three centuries: a dendrochronological analysis of inter-disturbance synergism. *PLoS ONE* 9:e114282.
- Gartner, M. H., T. T. Veblen, R. L. Sherriff, and T. L. Schoennagel. 2012. Proximity to grasslands influences fire frequency and sensitivity to climate variability in ponderosa pine forests of the Colorado Front Range. *International Journal of Wildland Fire* 21:562–571.
- Gavin, D. G. 2010. K1D: multivariate Ripley's K-function for one-dimensional data. http://geog.uoregon.edu/envchange/software/K1D_1.pdf
- Gavin, D. G., F. S. Hu, K. P. Lertzman, and P. Corbett. 2006. Weak climatic control of stand-scale fire history during the late Holocene. *Ecology* 87:1722–1732.
- Grassland Strategy Working Group. 2001. Cariboo-Chilcotin grasslands strategy: forest encroachment onto grasslands and establishment of a grassland benchmark area. Grassland Strategy Working Group, Williams Lake, British Columbia, Canada.
- Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205–221.
- Grissino-Mayer, H. D., and T. W. Swetnam. 2000. Century scale climate forcing of fire regimes in the American Southwest. *Holocene* 10:213–220.
- Hansen, A. J., and F. di Castri. 2012. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York, New York, USA.
- Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139.
- Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. *Landscape Ecology* 22:5–24.
- Hessburg, P. F., et al. 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. *Landscape Ecology* 30:1805–1835.
- Hessburg, P. F., et al. 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *Forest Ecology and Management* 366:221–250.
- Heyerdahl, E. K., R. F. Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. *Forest Ecology and Management* 230:107–118.
- Heyerdahl, E. K., K. P. Lertzman, and S. Karpuk. 2007. Local-scale controls of a low-severity fire regime (1750–1950), southern British Columbia, Canada. *Ecoscience* 14:40–47.
- Heyerdahl, E. K., P. Morgan, and J. P. Riser. 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), Northern Rockies, USA. *Ecology* 89:705–716.
- Heyerdahl, E. K., K. P. Lertzman, and C. M. Wong. 2012. Mixed-severity fire regimes in dry forests of southern interior British Columbia, Canada. *Canadian Journal of Forest Research* 42:88–98.
- Iverson, K. E., R. W. Gray, B. A. Blackwell, C. Wong, and K. L. MacKenzie. 2002. Past fire regimes in the Interior Douglas-fir, dry cool subzone, Fraser variant (IDFdk3). Report to the Innovative Forest Practices Agreement. Lignum, Williams Lake, British Columbia, Canada.
- Keane, R. E., P. F. Hessburg, P. B. Landres, and F. J. Swanson. 2009. The use of historical range and variability (HRV) in landscape management. *Forest Ecology and Management* 258:1025–1037.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18:116–126.
- Klenner, W., R. Walton, A. Arsenault, and L. Kremsater. 2008. Dry forests in the southern interior of British Columbia: historic disturbances and implications for restoration and management. *Forest Ecology and Management* 256:1711–1722.
- Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179–1188.
- Lepofsky, D., E. K. Heyerdahl, K. P. Lertzman, D. Schaepe, and B. Mierendorf. 2003. Historical meadow dynamics in southwest British Columbia: a multidisciplinary analysis. *Conservation Ecology* 7:5.
- Lessard, V. C., T. D. Drummer, and D. D. Reed. 2002. Precision of density estimates from fixed-radius plots compared to N-tree distance sampling. *Canadian Journal of Forest Science* 48:1–5.
- Marcoux, H. M., L. D. Daniels, S. E. Gergel, E. Da Silva, Z. E. Gedalof, and P. F. Hessburg. 2015. Differentiating mixed-and high-severity fire regimes in mixed-conifer forests of the Canadian Cordillera. *Forest Ecology and Management* 341:45–58.
- Miller, C., and D. L. Urban. 2000. Connectivity of forest fuels and surface fire regimes. *Landscape Ecology* 15:145–154.
- Miller, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17:2145–2151.
- Moore, R. D., D. L. Spittlehouse, P. H. Whitfield, and K. Stahl. 2010. Weather and climate. Pages 47–84 in R. G. Pike, T. E. Redding, R. D. Moore, R. D. Winker, and K. D. Bladon, editors. Compendium of forest hydrology and geomorphology in British Columbia. Ministry of Forests, Range and Natural Resource Operations, Victoria, British Columbia, Canada.
- Morgan, P., E. K. Heyerdahl, and C. E. Gibson. 2008. Multi-season climate synchronized forest fires throughout the 20th century, Northern Rockies, USA. *Ecology* 89:717–728.
- Nicholson, A., E. Hamilton, W. Harper, and B. Wikeem. 1991. Chapter 8: bunchgrass zone. Pages 125–137 in D. Meidinger, and J. Pojar, editors. *Ecosystems of British Columbia*. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- Odion, D. C., et al. 2014. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS ONE* 9:e87852.
- Oliver, C. D., and B. C. Larson. 1990. *Forest stand dynamics*. McGraw-Hill, New York, New York, USA.

- Parminter, J. V. 1978. An historical review of forest fire management in British Columbia. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.
- Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262:703–717.
- Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology* 194:5–16.
- Reich, P. B., D. W. Peterson, D. A. Wedin, and K. Wrage. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82: 1703–1719.
- Reid, J. 2008. The grasslands debates: conservationists, ranchers, first nations, and the landscape of the middle Fraser. *B.C. Studies* 160:93–118.
- Reid, J. 2010. Grassland debates: conservation and social change in the Cariboo-Chilcotin, British Columbia. Dissertation. University of British Columbia, Vancouver, British Columbia, Canada.
- Risser, P. G. 1995. The status of the science examining ecotones. *BioScience* 45:318–325.
- Rother, M. T., and H. D. Grissino-Mayer. 2014. Climatic influences on fire regimes in ponderosa pine forests of the Zuni Mountains, NM, USA. *Forest Ecology and Management* 322:69–77.
- Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the Environment* 11:e15–e24.
- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54:661–676.
- Sherriff, R. L., and T. T. Veblen. 2007. A spatially-explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. *Ecosystems* 10: 311–323.
- Sherriff, R. L., and T. T. Veblen. 2008. Variability in fire-climate relationships in ponderosa pine forests in the Colorado Front Range. *International Journal of Wildland Fire* 17: 50–59.
- Sherriff, R. L., R. V. Platt, T. T. Veblen, T. L. Schoennagel, and M. H. Gartner. 2014. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *PLoS ONE* 9:e106971.
- Sigafoos, R. H., and E. L. Hendricks. 1969. The time interval between stabilization of alpine glacial deposits and establishment of tree seedlings. US Geological Survey Professional Paper 650B:B89–B93.
- Soulé, P. T., and P. A. Knapp. 2000. *Juniperus occidentalis* (western juniper) establishment history on two minimally disturbed research natural areas in central Oregon. *Western North American Naturalist* 60:26–33.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:6053:230–232.
- Strang, R. M., and J. V. Parminter. 1980. Conifer encroachment on the Chilcotin grasslands of British Columbia. *Forestry Chronicle* 56:13–18.
- Swetnam, T.W., and C.H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11–32 in C. D. Allen, editor. *Fire Effects in Southwestern Forest: Proceedings of the 2nd La Mesa Fire Symposium*. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RM-GTR-286.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206.
- Tisdale, E. W. 1947. The grasslands of the Southern Interior of British Columbia. *Ecology* 28:346–382.
- Tisdale, E. W., and A. McLean. 1957. The Douglas-Fir zone of southern interior British Columbia. *Ecological Monographs* 27:247–266.
- Trouet, V., A. H. Taylor, E. R. Wahl, C. N. Skinner, and S. L. Stephens. 2010. Fire-climate interactions in the American West since 1400 CE. *Geophysical Research Letters* 37:1–5.
- Turner, N. J. 1999. Time to burn: traditional use of fire to enhance resource production by Aboriginal Peoples in British Columbia. Pages 185–218 in R. Boyd, editor. *Indians, fire and the land in the Pacific Northwest*. Oregon State University Press, Corvallis, Oregon, USA.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.
- Turner, J. S., and P. G. Krannitz. 2001. Conifer density increases in semi-desert habitats of British Columbia in the absence of fire. *Northwest Science* 75:176–182.
- Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10:1178–1195.
- Watson, E., and B. H. Luckman. 2004. Tree-ring based reconstructions of precipitation for the southern Canadian Cordillera. *Climatic Change* 65:209–241.
- Westerling, A. L., A. Gershunov, T. J. Brown, D. R. Cayan, and M. D. Dettinger. 2003. Climate and wildfire in the western United States. *Bulletin of American Meteorological Society* 84:595–604.
- Wilson, I. R. 1998. Archaeological Overview Assessment Northern Secwepemc Traditional Territory. Report Prepared for First Nations of Canim Lake, Canoe Creek, Soda Creek, Williams Lake.
- Wong, C. M., and K. P. Lertzman. 2001. Errors in estimating tree age: implications for studies of stand dynamics. *Canadian Journal of Forest Research* 31:1262–1271.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1563/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in NOAA National Centers for Environmental Information repository <https://www.ncdc.noaa.gov/paleo/study/21871>.